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Preliminary observations of behavioural thermoregulation in an elapid snake, the dugite, *Pseudonaja affinis* Gunther

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Abstract

Biotelemetry was used to study the behavioural thermoregulation of an adult dugite *(Pseudonaja affinis)* which was confined in a large external enclosure. At the start of digestion the dugite regulated its body temperature at 32.9 ± 0.21°C and this fell within a few days to 32.2 ± 0.09°C ($p < 0.01$) which appears to correspond to the range for the preferred body temperature (PBT) for this species. Throughout the period of observation the snake periodically allowed its body temperature to rise above the PBT, when exploring the enclosure or searching for food, and this often exceeded 34°C with 35.4°C being the maximum temperature voluntarily tolerated. As periods of thermoregulation and searching alternated throughout each day, the overall mean body temperature recorded was higher than the PBT and equalled 33.6 ± 0.23°C at the start and 32.4 ± 0.12°C at the end of the period of digestion.

Introduction

Studies of behavioural thermoregulation in reptiles have concentrated almost exclusively until recently on lizards (see Templeton 1970 for a review) but the development of suitable biotelemetric techniques has resulted in an increasing number of studies devoted to snakes (McGinnis and Moore 1969, Osgood 1970, Johnson 1972, Naulleau and Marquès 1973, Bui Ai *et al.* 1975, Saint Girons 1975, 1978, Shine 1976). However, information on the thermal preferences of Australian elapid snakes is extremely meagre and fragmentary (see Heatwole 1976 for a bibliography) and this motivated us to make some preliminary observations on a single large specimen of the dugite *(Pseudonaja affinis)* held in captivity in Perth, Western Australia.

Materials and methods

The observations were carried out on an adult male dugite *(Pseudonaja affinis)* captured on 9 November 1978 at the University of Western Australia's Marsupial Breeding Station at Jandakot. The snake was placed the next day in a large enclosure (3.5 x 2.5m) which had a sand base and was furnished with a variety of stone shelters and two large basins containing water. The enclosure was in the shade of surrounding trees each day between 0800 and 0855 h and from 1430 h onwards. Another smaller dugite and two tiger snakes *(Notechis ater)*, all captured on the same day at Jandakot, were also housed in the same enclosure. On 16 November the large dugite, which had settled down well in the enclosure and was no longer disturbed by the presence of observers, swallowed at 1045 h a dead mouse containing a temperature-sensitive radio transmitter (Model V, Mini-Mitter Co. Inc., Portland, Oregon). The dugite ate a second mouse at 0900 on 17 November and the observations were terminated at 1800 h on 20 November. The dugite was encouraged to regurgitate the transmitter by gentle manipulation and at this stage the second mouse was almost completely digested.

The transmitter was calibrated in water with a Schultheis thermometer, before and following its implantation in the dugite. The pulse rate varied linearly between 0°C and 50°C and the signal was received with a small commercial transistor radio. The number of pulses per 30 seconds were counted, using a stopwatch, and subsequently converted to give the body temperature of the animal. The transmitter used had a useful range of approximately 1m and antennae were placed on the ground inside the enclosure to facilitate reception of the signal when the dugite was moving about. In total, 181 measurements of the body temperature of the snake were recorded, 128 of these on 18 and 19 November when the animal was kept under continuous observation. Mean temperatures were calculated from the values recorded when the enclosure was in full sunlight and the animal was thus provided with a suitable gradient for thermoregulation. Data from periods when the enclosure was in shade are shown in Figure 1, but were excluded when calculating mean body temperatures.

The statistical significance of differences between mean body temperatures was assessed using Student's t-test and a probability of less than 0.05 was taken to indicate significance.

Results

The dugite emerged from its nocturnal shelter as soon as this was touched by the first rays of sunlight in the morning (at approximately 0715 h)

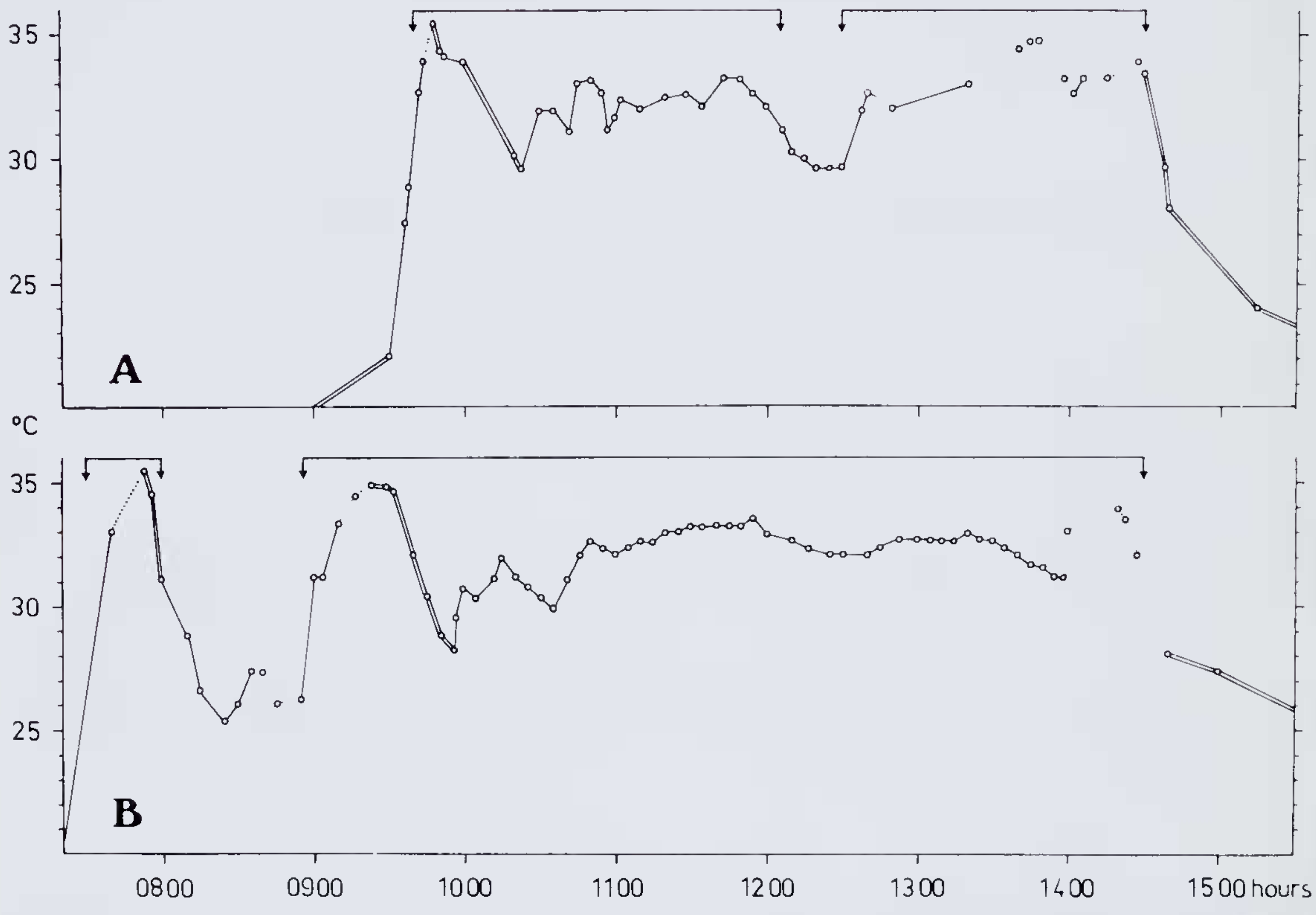

Figure 1.—Body temperature throughout the day of a large male dugite *(Pseudonaja affinis)* confined in an external enclosure on (A) 18 November 1978 and (B) 19 November 1978. The arrows (↓ ↓) indicate the times between which the enclosure was in full sunlight and the animal was thus provided with a large thermal gradient: (====) period when the snake was in its shelter; (———) periods when the snake was engaged uniquely in thermoregulatory behaviour; (.......) periods when the snake actively explored the enclosure in search of food

with a body temperature between 18°C and 22°C, depending upon the day. During most of the time when the sun was shining the animal was engaged in thermoregulatory activity, either resting in the shade or exposing a variable portion of its body to the sun's rays, usually at the entrance to its shelter. Under these conditions the body temperature did not vary by more than 3.6°C, the preferred body temperature (PBT) being 32.9 ± 0.30°C on 17 November, the day after swallowing a mouse, and this fell to 32.2 ± 0.37°C by 20 November by which time the process of digestion was much more advanced, the difference between these two means not being statistically significant (see Table 1). If however one compares the pooled mean for November 16 and November 17 (32.9 ± 0.21°C) with the overall mean for November 18-20 (32.2 ± 0.09°C), then this decline is statistically significant with $p < 0.01$.

Shade from nearby trees fell over the enclosure by 1430 h each day and the snake always returned to its shelter by 1500 h. Subsequently it would emerge infrequently and then only for brief periods in the late afternoon. At different periods of the day, usually between 0730 h and 1000 h and between 1300 h and 1500 h, the dugite would actively explore the enclosure attempting to burrow beneath all the stones and water containers. These activity periods, which were apparently motivated by a search for food, could be set off at any time of the day simply by the odour of a dead mouse and were observed at body temperatures ranging from 26.0°C to 34.9°C. During these periods the snake did not attempt to regulate its body temperature which consequently increased rapidly when the animal was in full sunlight up to a temperature of 35.4°C which corresponded to the maximum voluntarily tolerated. On reaching this temperature the animal would either move into the shade or, more often, return to its shelter whereupon its body temperature would fall rapidly, generally to a level much lower than the PBT, as if to compensate for the period of overheating. Only later would the dugite re-emerge partially and resume its normal thermoregulatory behaviour. Figure 1 gives a number of clear examples of such behaviour.

During nine such exploratory periods observed between 16-19 November, the mean body temperature of the dugite fell four times between 34.5 and 35.0°C and the mean recorded for the other five periods were respectively: 35.2°C, 34.3°C, 33.9°C, 32.1°C and 26.7°C. From these observations it would appear that such exploratory or food-seeking behaviour in the dugite is reasonably temperature-independent between the maximum voluntarily tolerated (35.4°C) and some minimum temperature which is probably

Table 1

Mean body temperatures (°C) and range for the dugite, Pseudonaja affinis, *during periods of exclusive thermoregulation (PBT) and overall, including exploratory and food-seeking, behaviour.*

Date (1978)	Preferred Body Temperature (PBT)	Range	Overall Mean Body Temperature	Range
16 Nov.	32·8 ± 0·15 (5)	32·3–33·2	33·7 ± 0·34 (10)	32·3–35·4
17 Nov.	32·9 ± 0·30 (12)	31·1–34·4	33·5 ± 0·31 (17)	31·1–35·4
18 Nov.	32·4 ± 0·67 (25)	31·1–33·2	32·8 ± 0·19 (40)*	29·6–35·4
19 Nov.	32·1 ± 0·95 (47)	29·6–33·5	32·3 ± 0·18 (64)**	28·0–35·4
20 Nov.	32·2 ± 0·37 (11)	31·5–32·9	32·2 ± 0·37 (11)*	31·5–32·9

Data given as mean ± S.E., number of observations in parentheses. Statistical significance of differences between means are given relative to the mean on the first day (16 November 1978) with * $p < 0·05$ and ** $p < 0·005$.

lower than 26°C. Such activity is limited nevertheless by the rapidity with which the animal attains its maximum temperature voluntarily tolerated during sunny periods of the day and this renders such exploratory activity virtually impossible during the hottest periods of the day, even in spring.

Since the body temperature tended to rise towards the maximum voluntarily tolerated whenever the animal was active and searching, the overall mean of all the body temperatures recorded when it was possible for the dugite to thermoregulate is almost certainly higher than the PBT. This overall mean was 33.6 ± 0.23°C for 16-17 November and 32.4 ± 0.12°C from 18-20 November (see Table 1), the difference between the two means being statistically significant with $p < 0.001$. The average PBT calculated at the beginning of the period of digestion (16-17 November) was 32.9 ±0.21°C and 32.2 ± 0.09°C over the period 18-20 November, when the period of digestion was more advanced, the difference between these two means being statistically significant with $p < 0.005$.

Discussion

In their now classic study of the behavioural thermoregulation of desert reptiles, Cowles and Bogert (1944) recognised a "basking range" and a "normal activity range" falling between the minimum and maximum temperatures voluntarily tolerated. Within the normal activity range they identified a "preferred" body temperature (PBT) for each species, which they also called the optimum or "eccritic" body temperature, corresponding to the mean of the body temperatures recorded when the animal is provided with a sufficiently extensive temperature gradient. Subsequently, many workers (e.g. Brattstrom 1965) have tended to confuse this PBT with the average body temperature of animals captured randomly throughout the day in the field, and taken usually with little regard for the specific behaviour of the animal at the time. Heath (1964) and Licht *et al.* (1966) where amongst the first to point out that such average body temperatures are misleading, comprising as they do, measurements from animals involved in a variety of activities, including basking when the body temperature has not yet attained the PBT. In many cases, although the animals may be active, the prevailing conditions may also be such that it is impossible for them to attain their PBT and Licht *et al.* (1966) and Bradshaw and Main (1968) noted a number of discrepancies between such field body temperatures and the temperature chosen by the same animals in a photothermal gradient in the laboratory. The problems associated with the measurement of the PBT are now better appreciated and have been recently discussed in the literature (see Saint Girons 1975, Heatwole 1976, Werner and Whitaker 1978).

In the case of *Pseudonaja affinis*, it is clear that so long as the snake is provided with a sufficiently broad thermal gradient it will maintain its body temperature within relatively narrow limits and the PBT of the animal studied varied little over a period of five days, being approximately 33°C at the beginning of digestion and 32°C at the end. The minimum temperature voluntarily tolerated is almost certainly lower than the lowest temperature recorded during the study (18°C) and the normal activity range for the dugite would appear to be between 26°C and 35.4°C, the latter representing the highest temperature voluntarily tolerated by this individual. Obviously the study of further individuals will modify this range somewhat but the above are probably reasonable estimates of these parameters for this species. The temperature range is very close to that of *Coluber flagellum (Masticophis flagellum)*, a diurnal Colubridae living in comparable semi-arid regions of the Mediterranean, for which Cowles and Bogert (1944) found a normal activity range from 27 to 35°C, a PBT of 33°C and a maximum temperature voluntarily tolerated of 37°C. Other specific comparisons are difficult to make, because of the variety of techniques employed by various workers and the frequent confusion between the PBT and the average field temperature of active animals, but it would appear that diurnal colubrids and elapids such as *Coluber flagellum* and *Pseudonaja affinis*, which actively hunt their prey in hot arid and semi-arid environments, have relatively elevated PBTs falling between 32 and 34°C (e.g. *Salvadora exalepis*, Jacobson and Whitford 1971, *Pseudonaja textilis*, Witten 1969). The rest of the Colubroidea, regardless of whether they are species from temperate regions, which are invariably diurnal and heliothermic no matter what their mode of life, or species such as the desert vipers which move mainly at night and surprise their prey, have a PBT between 30 and 32.5°C (Cowles and Bogert 1944, Saint Girons and Saint Girons 1956, Witten 1969, Shine 1976, Spellerberg and Phelps 1975, Heatwole 1976, Saint Girons 1978). The temperature preference of the Natricinae living in temperate regions appear to be even lower with PBTs falling between 27 and 30°C (Stewart 1965, Kitchell 1969, Osgood 1970, Gehrmann 1971). The few data published on snakes living in intertropical forests, most of which are not heliothermic, are difficult to interpret at this stage but it seems likely because of the high nocturnal temperatures characteristic of this environment that they also have low PBTs, as is the case with lizards inhabiting the same biotope (Ruibal and Philibosian 1970).

When they are preoccupied with activities such as food-seeking or courtship, heliothermic reptiles abandon to some extent their habitual precise thermoregulation. The minimum temperature voluntarily tolerated under these circumstances varies somewhat according to the type of activity in which the animal is engaged and can differ considerably from that measured for example at the beginning of the basking period. The maximum temperature voluntarily tolerated on the other hand appears to represent for the animal an upper physiological limit which cannot be exceeded, no matter what the activity. In temperate regions, exploratory behaviour or food-seeking is usually accompanied by a progressive fall in the body temperature to below the PBT whereas the reverse is the case with snakes living in hot arid regions which already have a PBT close to the upper limit of the normal activity range, and usually only a few degrees away from the maximum temperature voluntarily tolerated. This "overheating" during periods of more intense activity is particularly clear in the case of *Pseudonaja affinis* and, as a result, the mean body temperature of the snake during the sunny hours of the day was often as much as 1C° above the animal's PBT. It is possible that the rather high mean body temperature reported by Webb (1973, cited by Shine 1976) for the snake *Pseudonaja textilis* in an outdoor enclosure is due to the same phenomenon.

It is well established that European vipers, and probably the great majority of snakes, display thermal compensation when necessary. For example, during days with intermittent sunshine, vipers will manage to attain their PBT by a series of long basking periods in which they allow their body temperature to rise, almost to the maximum voluntarily tolerated, following periods of forced cooling when the sun is obscured by cloud (Saint Girons 1975). In hot regions this form of thermal compensation obviously functions in the opposite sense. Thus, after a period of exploration during which the body temperature of *Pseudonaja affinis* would rise to over 35°C, the snake would return to its shelter and allow its temperature to fall below 30°C before recommencing normal thermoregulation. It is also possible that this habitual exposure to elevated body temperatures permits arid-living species such as the dugite to retain a relatively low PBT, which is only of the order of 1 or 2C° higher than that of nocturnal species which lie in wait for their prey, despite their obvious thermophilia. This underlines the importance of knowing, in studies of comparative thermoregulation, not only the PBT, which is readily determined in a temperature gradient in the laboratory, but also the actual body temperatures to which the animals are exposed in the field.

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